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Radersma, Reinder; Tinbergen, Joost M.; Komdeur, Jan

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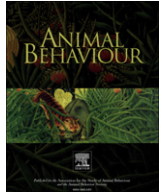
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Do brood sex ratio, nestling development and sex affect fledging timing and order? An experimental study on great tits

Reinder Radersma*, Joost M. Tinbergen, Jan Komdeur

Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen

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The process of nest leaving (fledging) in hole-breeding passerines is largely unexplored, although it is potentially an important facet of reproduction. We used the great tit, *Parus major*, to investigate whether fledging timing and order were affected by nestling development and sex, as well as the sex ratio in the brood the nestlings were raised in. Because of the difference in size and competitiveness between male and female nestlings, we expected to find an effect of sex and brood sex ratio (BSR) on the process of fledging. To explore its effect on fledging experimentally, we manipulated BSR by swapping 6-day-old nestlings of both sexes. We implanted transponders in all 14-day-old nestlings to determine timing and order of fledging. The brood age at fledging was best explained by average wing length of the brood (negative), average body mass of the brood (positive) and hatching date (negative). In contrast to our hypothesis, BSR did not affect fledging time. Also, the asynchrony of fledging within broods did not depend on BSR. Within broods, fledging order was not affected by sex or by the interaction between sex and BSR. Nestlings with long wings on day 14 fledged earlier than nestmates with shorter wings. Although females were lighter at day 14, they had similar length wings as their male nestmates. Nestlings should keep up with their nestmates during development, because developmental status relative to nestmates, rather than sex-specific competition, influenced the process of fledging.

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Although nest leaving (fledging) is the most drastic transition between habitats in the life of a passerine altricial bird, the process of fledging has been studied much less extensively than other facets of reproduction. This discrepancy is partly caused by the difficulty of predicting the moment of fledging and therefore the ability to observe the process (Johnson et al. 2004). The few studies on the process of fledging generally report that fledging of a brood starts when one of the nestlings reaches a certain threshold wing development (marsh tits, *Poecile palustris*, and pied flycatchers, *Ficedula hypoleuca*: Nilsson & Svensson 1993; tree swallows, *Tachycineta bicolor*: Michaud & Leonard 2000; pied flycatchers: Kern et al. 2001). Parental manipulation, in which parents try to force their offspring to leave the nest by depriving them of food (Johnson et al. 2004) or by displaying food in front of the nest (Michaud & Leonard 2000), is thought to play a minor role in the process of fledging (Nilsson 1990; Johnson et al. 2004).

In the only other study on the fledging process in great tits, *Parus major*, the order of fledging depended on nestling body mass

relative to that of the nestmates. Nestlings with an average body mass left the nest first, shortly thereafter followed by the heaviest nestlings and eventually followed by the lightest ones (Lemel 1989). The author hypothesized that (average-weight) subordinate nestlings try to evade competition with the (heaviest) dominant siblings by fledging first. Moreover, the lightest nestlings followed despite not being ready to fledge, to avoid starvation, because parental visits to the nest decreased drastically once most nestlings fledged (Lemel 1989). In contrast, studies in other passerines have found that fledging order correlates with wing development rather than body mass. Nestlings with the best developed wings fledge first (marsh tits: Nilsson 1990; tree swallows: Michaud & Leonard 2000; house wrens, *Troglodytes aedon*: Johnson et al. 2004).

So, generally, fast-developing broods and individuals stay in the nest for less time than slower-developing broods and individuals. We therefore hypothesize that faster-developing broods fledge earlier than slow-developing broods and faster-developing individuals leave the nest before slow-developing individuals. Two important aspects that are not covered by previous studies on timing and order of fledging are the influence of nestling sex and brood sex ratio (BSR). In great tits, male fledglings are 4% heavier than female fledglings (Nicolaus et al. 2009). There is no sexual size dimorphism at hatching, but sexual size dimorphism gradually

* Correspondence: R. Radersma, Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands.

E-mail address: radersma@caprea.nl (R. Radersma).

increases during the nestling phase. Because male nestlings are fed at the same rate as female nestlings (Michler et al. 2010), males either digest food more efficiently or allocate more resources to growth, than females do. We therefore expect males to reach the threshold state of development, and to fledge, earlier than females. We also expect male-biased broods to fledge earlier than female-biased broods. Fledging asynchrony is expected to be larger in mixed broods and, within broods, males should leave the nest before females.

When sex-specific size dimorphism leads to differences in the competitiveness of both sexes, expectations slightly change. Male nestlings might have a competitive advantage over female nestlings for access to food, because of the sexual size dimorphism (Oddie 2000). This competitive advantage is especially present under food-limited conditions, as experimentally shown by Oddie (2000). Sex-specific differences in competitive ability are hypothesized to result in more severe and competitive rearing conditions in broods with a male-biased BSR than in broods with a female-biased BSR (Uller 2006). Since fledging can be seen as a way to evade competition (Lemel 1989), we might expect fledging to be initiated earlier in the more competitive male-biased broods than in the less competitive female-biased broods. As a consequence of the relatively early initiation of fledging in male-biased broods, we predict more nestlings to be physically unprepared to fledge in male-biased broods. These nestlings should delay their own fledging, and therefore we expect greater fledging asynchrony in male-biased broods than in female-biased broods.

With this experimental study on the great tit, we sought to investigate whether nestling development, nestling sex and BSR determined timing and order of fledging. In addition, we investigated which other characteristics of broods (brood size, hatching date, sex of first fledgling and the averages of all individual traits) and individuals (wing length, tarsus length and body mass) were related to timing and order fledging.

METHODS

Data Collection

We focused on 25 first broods of the great tit from the Lauwersmeer (53°20'N, 06°12'E) population in the Netherlands in 2007. First broods are defined as broods in which the first egg was laid no later than 30 days after the laying of the first egg of the earliest clutch of the population in 2007 (6 April) and which were not replacement broods after a failed breeding attempt. Potential replacement broods were characterized by being slightly later than most broods, in combination with a very short nest-building phase, and were excluded from the analysis. Some of the potential replacement broods were definitely identified as replacement broods, because the colour-ringed female had been seen earlier with a failed brood.

The research area consists of 600 nestboxes spread over 12 areas with 50 nestboxes each: 47.8% of these were occupied by great tits in 2007. From the beginning of April onwards, we checked all nestboxes on a weekly basis to estimate the laying date of the first egg (back calculated under the assumption that one egg was laid per day) to determine clutch size and to predict hatching date. Two days before the predicted hatching date, we checked the nestbox daily to determine the actual hatching date of the first nestling. This date is taken as the hatching date of the complete brood (day 0). Two days after the hatching date, all nestlings were individually marked by nail clipping and a small blood sample (ca 5–10 µl) was taken from the tarsal vein for molecular sex determination (Griffiths et al. 1998). When not all eggs were hatched by day 2, we visited the nest daily until day 6 to mark and to take a blood sample

from the late-hatched nestlings. On day 5 all nestlings were counted and missing individuals were identified and noted. On day 6 all nestlings were weighed with a spring balance to the nearest 0.1 g, later referred to as body mass at day 6 (BM₆), and banded for individual identification. Subsequently, nestlings from nests of the same age were swapped (brought from one nest to another) to get an experimental range of BSRs, and eggs that did not hatch were removed. The nestlings were kept warm with heat pads and transported by car. The whole swapping process took less than 30 min for an individual nestling. At least one nestling per nest was swapped to control for swapping effects. After swapping, all broods had at least one individual of each sex. The BSRs were either female biased (approximately 25% males), male biased (approximately 75% males) or balanced (approximately 50% males). The female- and male-biased BSRs corresponded to approximately 1.3 times the standard deviation from a balanced BSR. This study took place in the context of a larger project, in which not only BSRs but also brood sizes were changed. Because we could not select enough broods with an unchanged brood size, we included broods that were increased or decreased at most by only one nestling. This study included 11 nests with a brood size reduction of one, 10 nests with a brood size increase of one and four nests with an unchanged brood size. The brood size change did not influence the results (see Results).

When the oldest nestling of a nest was 14 days old, all nestlings were weighed to the nearest 0.1 g (BM₁₄), the tarsus (TL₁₄) was measured to the nearest 0.1 mm, and the length of the third primary feather was measured to the nearest 0.5 mm by using a stop ruler (WL₁₄). A passive integrated transponder (Trovan ID100, www.trovan.com; 2.1 × 11.5 mm, 0.1 g, 0.5–1% of BM₁₄) was implanted subcutaneously above the shoulder blade according to the method described in Nicolaus et al. (2008). Also at day 14 we placed at the nestbox entrance an antenna attached to a reading device (Trovan 665), which registered the date and time of fledging of each individual in the nest and, therefore, the fledging order as well. From day 19 onwards, nestboxes were checked every second day to see whether the young had fledged. After the completion of fledging, the antenna and reading device were removed, and the nestbox was cleared to check for dead nestlings in the nest material. The data from the reading device were downloaded with Trovan LID650/665 software version 603.

Data Analyses

Below, individual characteristics, which were averaged within broods, are marked by the prefix 'brood'. The standard deviations from the means of individual characteristics within broods are marked by the prefix 'brood SD'. The age at fledging was calculated as the number of days between the day the first egg in a nest hatched and the day the focal nestling fledged. This leads to an overestimation of the age of late-hatched nestlings. However, within-brood differences in hatching age occur naturally. This will probably result in differences in size and development, which might have implications for the fledging order, but since we were interested in finding out how variation in different growth factors (as well as sex and BSR) affects variation in fledging age and order, we see the variation in the moment of hatching as a source of variation in growth. We therefore took into account the variation in hatching moment in the different growth factors. For sex-specific hatching order, the overestimation of the age of late-hatched nestlings might influence fledging order or age, but late-hatched nestlings (individuals born at least 2 days later than the first-hatched nestling in a brood) had the same probability of being either male or female as the other nestlings in this study population in 4 consecutive years (2005: $\chi^2_1 = 0.64$, $N = 2283$, $P = 0.42$; 2006:

$\chi^2_1 = 0.16$, $N = 2139$, $P = 0.96$; 2007: $\chi^2_1 = 1.02$, $N = 2373$, $P = 0.31$; 2008: $\chi^2_1 = 1.96$, $N = 1800$, $P = 0.33$). Brood age at fledging was the mean fledging age of all young within a brood. The individual age at fledging is always given in whole days, but the brood age at fledging is not because this is expressed as mean age (in days).

We calculated a fledging asynchrony parameter, which is a measure for the spread in the timing of fledging observed in a brood. This parameter allowed us to compare the asynchrony between broods. To calculate fledging asynchrony, we took for all fledglings the time (h) between the fledging of the first fledged nestmate and the focal fledgling and calculated the standard deviation of these differences per brood. We also looked at fledging asynchrony by comparing the logarithm of the time between fledging of two subsequent individuals with their difference in WL_{14} . Since nestlings do not fledge at night, we subtracted the time between sunset and sunrise from the time difference when there was a night between fledging of the two nestlings. This measure was transformed by adding 1 and taking the natural logarithm to make it normally distributed. The fledging asynchrony is defined as the within-brood standard deviation of the above-described values.

To compare broods of different sizes, we linearly transformed the fledging ranks to values varying from 0 to 1, with 0 for the first and 1 for the last-fledged individual. These linearly transformed values are referred to as fledging order, while the ranks are referred to as fledging ranks. To compare nestlings within broods, we calculated relative WL_{14} (WL_{14} minus the mean brood WL_{14}) and relative BM_{14} (BM_{14} minus the mean brood BM_{14}).

We tested whether the first fledgling leaving the nest might thereby avoid monopolization of the food by its nestmates sitting in the nest opening, as proposed by Lemel (1989). We calculated for each individual the proportion of time spent in the nestbox opening. A bird sitting continuously in the nest opening was read every 3 s by the reading device, and we used the number of these readings to estimate this proportion of time. We ranked these proportions within broods (highest proportion first) and referred to them as monopolization ranks.

Two families of general linear models were used for the analyses. In the first model family we tried to explain the between-brood variation in brood age of fledging by means of brood characteristics (see Results for the full list). In the second model family we tried to explain the fledging order within broods. In this case we used both individual and brood characteristics (see Results for the full list). In model family 2, we introduced a factor 'swap', which equalled 1 for swapped nestlings and 0 for other nestlings. Brood age at fledging showed a normal distribution, but the distribution of fledging order was uniform. Fledging order, however, was not skewed ($t_{174} = 0.00$, $P = 0.500$) and the best model explaining fledging order did not show heteroscedasticity ($\chi^2_{132} = 144.6$, $P = 0.213$). Since general linear models are rather insensitive to distributions deviating from normality (Gelman & Hill 2007), we constructed general linear models to explain fledging order. For both model families, all continuous variables were inserted in the model as z scores (normalized, centred and divided by the SD) to compare the effect size of the variables in the model. To normalize hatch date, we performed an inverse transformation. The z scores of the relative WL_{14} and the relative BM_{14} were calculated by subtracting the average z score within a brood from the individual z score.

The statistical full models of the two model families were constructed in R (R Development Core Team 2009) with the package 'arm' (Gelman et al. 2009). Using a classical backwards elimination method, the best-fitting statistical models were constructed. We rejected variables with the highest P value one by one, until all variables had a P value smaller than 0.05. We report nonsignificant parameters retested after elimination in the final model.

Ethical Note

To investigate whether the swapping procedure had any adverse effects on the nestlings, we investigated whether swapping affected BM_{14} or survival until day 14. Swapped nestlings were not lighter at day 14 ($F_{1,192} = 0.131$, $P = 0.254$) and did not survive less well until day 14 ($F_{1,207} = 0.001$, $P = 0.975$) than nestlings that were not swapped to another brood. In 2004 we conducted a survey to investigate whether taking blood samples from 2-day-old nestlings had any adverse effects. We took blood samples from about 60% of the nestlings in the study population. Nestlings from which blood samples were taken were not lighter at day 14 ($t_{1320.6} = 0.66$, $P = 0.51$) and did not survive less well until day 14 ($t_{1484.4} = -0.021$, $P = 0.98$). In a previous study in the same population no adverse effects of the implantation of passive integrated transponders were found on fledging success, winter condition, survival or recruitment (Nicolaus et al. 2008).

The study was carried out with the approval of the Institutional Animal Care and Use Committee of the University of Groningen.

RESULTS

Brood Characteristics

The average brood age at fledging \pm SD was 19.6 ± 1.3 days ($N = 25$). The difference in time of fledging between the first and the last young within a nest ranged from 7 min 13 s to 2637 min (about 44 h; 28 h when we subtracted the time between sunset and sunrise) and showed a log normal distribution with an average \pm SD of $e^{4.91 \pm 1.79}$ min (about 136 min). A small number of nestlings died between days 6 and 14 (5.7%, 11 of 194) and between day 14 and fledging (4.4%, 8 of 183). Mortality within a brood was not affected by BSR ($F_{1,23} = 0.077$, $P = 0.784$) or by brood size ($F_{1,23} = 0.157$, $P = 0.696$).

Individual Characteristics

WL_{14} and BM_{14} were positively associated ($F_{1,173} = 81.8$, $P < 0.001$). Males were heavier than females (BM_{14}), but the sexes did not differ in wing length (WL_{14} ; Table 1). We did not find any differences between swapped and nonswapped individuals in the following nestling traits: BM_6 ($F_{1,173} = 0.412$, $P = 0.522$), BM_{14} ($F_{1,173} = 1.61$, $P = 0.207$), WL_{14} ($F_{1,173} = 1.15$, $P = 0.286$), TL_{14} ($F_{1,173} = 0.317$, $P = 0.574$), relative BM_{14} ($F_{1,173} = 1.64$, $P = 0.202$), relative WL_{14} ($F_{1,173} = 0.052$, $P = 0.821$) and monopolization rank ($F_{1,173} = 0.003$, $P = 0.960$).

The nest entrance monopolization ranks were positively correlated with fledging ranks (Fig. 1). The more a nestling sat in the nestbox opening, compared to its nestmates, the higher the chance that it fledged first.

Brood Age at Fledging

The variance in brood age at fledging was not explained by the variance in BSR ($F_{1,23} = 0.583$, $P = 0.453$). The best model explaining

Table 1

Average \pm SD day 14 body mass (BM_{14}), day 14 wing length (WL_{14}) and fledging order (between 0 and 1, see Methods) of male and female nestlings in the Lauwersmeer great tit population and the differences between the sexes in these traits

	Males ($N=85$)	Females ($N=90$)	Sex-specific differences			
			Difference	t	df	P
BM_{14} (g)	16.07 ± 1.91	15.39 ± 1.41	0.68	-2.660	153.944	0.009
WL_{14} (mm)	29.72 ± 3.57	29.61 ± 3.68	NS	-0.192	172.873	0.848
Fledging order	0.53 ± 0.35	0.47 ± 0.33	NS	-1.070	170.681	0.285

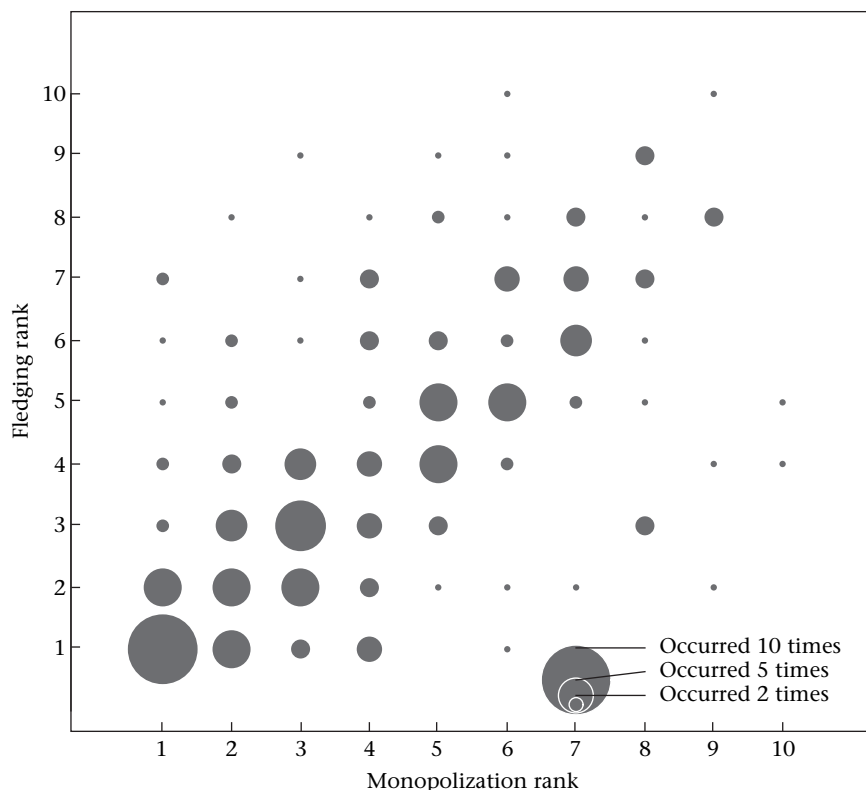


Figure 1. The rank of monopolization of the nestbox opening against the fledging rank of nestlings in broods of the Lauwersmeer great tit population. The radii of the bubbles represent the number of times a monopolization rank/fledging rank combination occurred. Monopolization rank and fledging rank were correlated ($r = 0.559$, $t_{177} = 8.88$, $P < 0.001$).

the brood age at fledging included brood WL₁₄, hatching date and brood BM₁₄ as explanatory variables (Table 2, Fig. 2). An increase in brood WL₁₄ by 1 SD (=2.7 mm) resulted in a decrease in brood age at fledging of 1.04 SD (=1.3 days). An increase in the average hatching date by 1 SD (=3.4 days) resulted in an increase in brood age at fledging by 0.36 SD (=0.45 days). A decrease in the average hatching date by 1 SD (=3.8 days) resulted in a decrease in brood age at fledging by 0.36 SD (=0.45 days). An increase in brood BM₁₄ by 1 SD (=1.3 g, and controlled for WL₁₄ and hatching date) resulted in an increase in brood age at fledging of 0.45 SD (=0.58 days).

Fledging Asynchrony

Fledging asynchrony was not affected by BSR ($F_{1,23} = 0.182$, $P = 0.674$), by brood SD WL₁₄ ($F_{1,23} = 0.218$, $P = 0.645$) or by brood SD BM₁₄ ($F_{1,23} = 0.320$, $P = 0.577$). We did find a close to significant association between the difference in WL₁₄ between two subsequent fledging nestmates and the natural logarithm of the difference in their fledging times ($F_{1,148} = 3.82$, $P = 0.052$).

Fledging Order

The fledging order (within broods) was not affected by sex alone ($F_{1,173} = 1.15$, $P = 0.284$) or by the sex*BSR interaction ($F_{1,171} = 0.521$, $P = 0.471$). Both relative WL₁₄ ($F_{1,173} = 49.5$, $P < 0.001$) and relative BM₁₄ ($F_{1,173} = 27.8$, $P < 0.001$) were associated with fledging order. Whether an individual was swapped or not was almost significantly associated with fledging order ($F_{1,173} = 3.36$, $P = 0.068$). The best model explaining fledging order included only relative WL₁₄ (Table 3, Fig. 3). An increase in relative WL₁₄ by 1 SD (=2.67 mm) resulted in a decrease in fledging order by 0.214 (1.7 places forward in the fledging order for a brood of eight young).

DISCUSSION

In this study we did not find any support for BSR or nestling sex affecting fledging order or timing. The experimentally changed BSR did not affect brood age at fledging. Fledging asynchrony did not

Table 2

Best model for explaining average brood age at fledging in the Lauwersmeer great tit population

Age at fledging	Variable	Estimate	SE	<i>t</i>	<i>P</i>
Final model	Intercept	~0	0.125	~0	1.000
	Brood WL ₁₄	-1.037	0.175	-5.94	<0.001
	Hatching date [†]	-0.355	0.139	-2.56	0.018
	Brood BM ₁₄	0.449	0.178	2.52	0.020
Rejected terms	Sex first fledging [‡]	-0.315	0.253	-1.24	0.229
	Change in brood size	-0.137	0.140	-0.977	0.340
	BSR	-0.080	0.135	-0.594	0.559
	Brood TL ₁₄	-0.131	0.215	-0.590	0.562
	Brood BM ₆	-0.083	0.185	-0.448	0.659
	Brood size	0.017	0.143	0.119	0.906
	Treatment [§]				
	Female biased	0.138	0.321	0.430	0.672
	Male biased	-0.004	0.341	-0.013	0.990
	Sex first fledging [‡] *BSR	-0.109	0.315	-0.344	0.735

All variables were normalized, centralized (minus the average) and standardized (divided by the SD), except for the factorial variables sex first fledging and treatment. All rejected variables were tested separately in the final model. WL₁₄: day 14 wing length; BM₆: day 6 body mass; BM₁₄: day 14 body mass; TL₁₄: day 14 tarsus length; BSR: brood sex ratio.

[†] To normalize hatching date we performed an inverse transformation; therefore the negative effect of the *z* score corresponds to a positive effect of the real hatching date.

[‡] Where 1 is male and 0 is female.

[§] Effect of more female-biased broods and male-biased broods compared to broods with a balanced BSR.

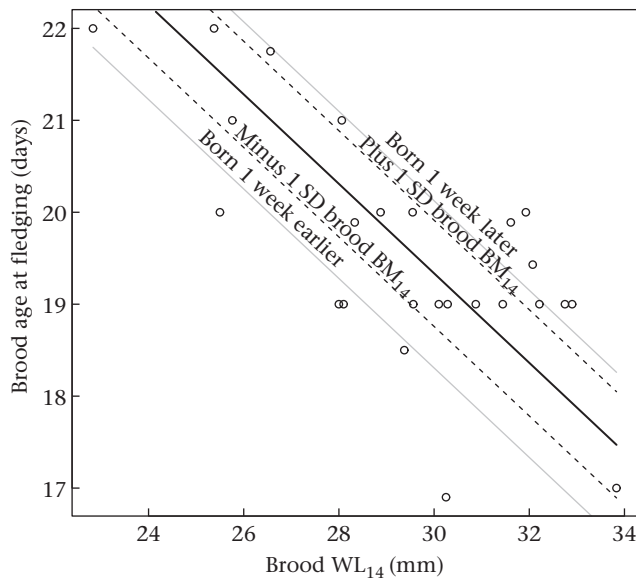


Figure 2. Brood wing length at day 14 as a function of the mean age at fledging (for mean brood body mass at day 14, BM_{14} , and mean date of birth) of broods in the Lauwersmeer great tit population. The upper dashed line represents the same function when brood BM_{14} is 1 SD above average (+1.3 g) and the lower dashed line represents the same function when brood BM_{14} is 1 SD below average (-1.3 g). The upper grey line represents the same function when date of birth is 1 week later than average and the lower grey line represents the same function when date of birth is 1 week earlier than average. Data points are raw data; regression lines are back transformed from the model.

depend on BSR and fledging order did not depend on nestling sex or the sex*BSR interaction. In contrast to our expectations, sex-specific competition seemed to have little impact on the process of fledging. We did find, however, that wing development was important. The brood age at fledging (around day 19) was negatively associated with brood wing length at day 14 and positively associated with brood body mass and hatching date. Although we did not find fledging asynchrony to be affected by the variation in wing length in the nest, we found the time between the fledging of two successive fledglings was almost significantly associated with the difference in their wing development. The fledging order was negatively associated with the relative wing length. This makes it more likely that developmental status rather than sex-specific competition influences the process of fledging.

Table 3

Best model for explaining the fledging order in broods of the Lauwersmeer great tit population

Fledging order	Variable	Estimate	SE	t	P
Final model	Intercept	0.500	0.022	22.31	<0.001
	Relative WL_{14}	-0.214	0.031	-7.033	<0.001
Rejected terms	Swap†	0.100	0.051	1.952	0.052
	Relative BM_{14}	-0.080	0.041	-1.922	0.056
	Sex‡	0.056	0.045	1.244	0.215
	Sex‡*BSR	0.032	0.050	0.634	0.527
	Sex‡*Relative WL_{14}	0.019	0.061	0.313	0.755
	Sex‡*Relative BM_{14}	-0.017	0.072	-0.233	0.816

All variables were normalized, centralized (minus the average) and standardized (divided by the SD), except for the factorial variables swap and sex. All rejected variables were tested separately in the final model. WL_{14} : day 14 wing length; BM_{14} : day 14 body mass; BSR: brood sex ratio.

† Where 1 is swapped and 0 is nonswapped individual.

‡ Where 1 is male and 0 is female.

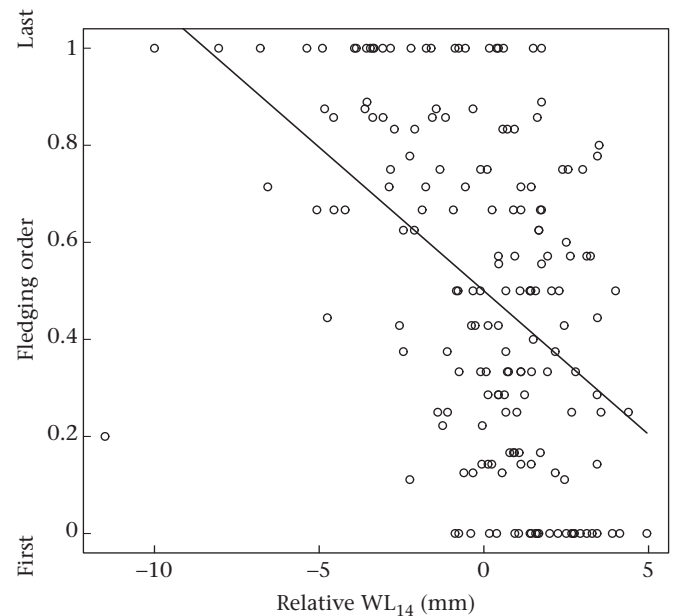


Figure 3. Fledging order as a function of relative wing length at day 14 of nestlings in broods of the Lauwersmeer great tit population. Data points are raw data; the regression line is back transformed from the model.

Brood Age at Fledging

The best statistical model describing brood age at fledging included a negative association with brood WL_{14} . Broods that showed less developed wings at 14 days remained longer in the nest than more developed broods. This is in agreement with several other studies on passerines (Nilsson & Svensson 1993; Michaud & Leonard 2000; Kern et al. 2001). Our finding supports the idea that young fledge after they have reached a certain threshold state of development (Johnson et al. 2004). Because less well-developed broods (at day 14) took extra time before fledging (at around day 19), they might have partly made up for their delay in development at the moment of fledging.

The reason why wing development determines the brood age of fledging might be that nestlings try to keep the risk of mortality low. Fledging can be seen as a transition from one habitat to another, from inside to outside the nest. A strong selection pressure can be expected on being prepared for the new habitat at the moment of transition. In great tits, fledglings are subject to a high mortality rate just after leaving the nest. This mortality is probably mainly due to predation (Naef-Daenzer et al. 2001). A negative relationship between mortality rate just after fledging and wing development at fledging would select for fledging with better developed wings. In natural cavities hole-breeding passerines face a high risk of nest predation (20–55% of the nests in collared flycatchers, *Ficedula albicollis*: Walankiewicz 2002; Mitrus 2003). This led us to hypothesize that nestlings leave the nest because predation risk outside will eventually become lower than the expected predation risk inside the nest. This hypothesis is consistent with the association between brood WL_{14} and brood age at fledging we observed, assuming the predation risk in the nest, expected by the birds, is constant over time and between nestboxes.

An alternative explanation, supported by the association between brood WL_{14} and brood age of fledging, is that sibling competition might cause fledging. The largest and most dominant nestling in a nest benefits from maintaining its prime feeding position, but in the course of time, the other nestlings catch up in

body mass and size, because body mass gain levels off prior to fledging. As such, the prime position of the dominant nestling is challenged more and more. To ensure its prime position, the largest nestling is forced to leave the nest, because parents tend to feed fledglings over nestlings (Nilsson & Svensson 1993).

Apart from the negative association between brood age at fledging and brood WL₁₄, age at fledging was positively associated with hatching date. Various studies have shown that nestling growth rate decreases over the breeding season, as a consequence of changes in food abundance (e.g. Naef-Daenzer & Keller 1999). In our study, this decrease in growth rate cannot be the sole reason for the date effect, because we controlled for the brood BM₁₄ and the brood WL₁₄. There must be an additional reason why nestlings fledge at an older brood age later in the season. It could be that the lower food abundance later in the season (Van Balen 1973; Van Noordwijk et al. 1995) makes it more difficult for the parents to find food. A higher mobility of the fledglings will therefore be more beneficial, since this will increase the food intake rate. When mobility depends on wing development, we can expect that individuals fledging later in the season need better developed wings once outside the nest. Alternatively, fledglings need better wing development outside the nest later in the season because of predation. Individuals that fledge later in the season have a higher risk of being predated (Geer 1982; Götmark 2002). This increase is believed to relate to the fact that predators (e.g. sparrowhawks, *Accipiter nisus*) synchronize their reproduction to the fledging peak of their prey (e.g. great tits), leading to an increase in predator food consumption over the breeding season (Götmark 2002). At the same time frequency-dependent selection on wing development caused by predation might play a role. If fledglings improve their predator avoidance skills with age, the fraction of fledglings with poor skills will decrease over the breeding season, because later in the season a larger fraction of fledglings is experienced. Late-fledged individuals will therefore be more vulnerable to predation, because they are less experienced than the earlier fledging individuals, which makes them the easy prey (Geer 1982). Therefore it might be adaptive for late-born fledglings to stay longer in the nest and to develop their wings better to increase their ability to fly and avoid predation, assuming that predation in the nest stays constant or increases at a slower rate over the season.

The positive relation between fledging age and hatching date might indicate a decrease in sibling competition in the nest over the season. This might be caused by a decrease in brood size over the season (Kluijver 1951; Perrins 1965), although we would then expect brood size to contribute to the best model instead of hatching date. The increase in variation in development within a nest might reduce sibling competition over the season, since the prime feeding position of the best developed nestling will be less challenged.

In addition to hatching date, brood BM₁₄ had a positive effect on age at fledging, when controlled for brood WL₁₄. Broods that were relatively heavy for their wing development stayed in the nest longer than broods that were relatively light. A high wing loading (body mass per wing area) negatively influences flight performance (Pennycuik 1975). Therefore, broods that are relatively heavier for their wing size may need to stay longer in the nest to grow larger wings. Larger wings reduce the wing loading and ensure sufficient flight performance when fledging. This would be advantageous for escaping predation, improving mobility and increasing foraging ability. We do not expect a reverse causality, in which broods that stay longer in the nest become relatively heavy for their wing development, because body mass stabilizes before day 14 (so more than 5 days prior to fledging), while wing length keeps increasing after day 14 (Orell 1983).

In the best model explaining brood age at fledging, both brood WL₁₄ and brood BM₁₄ were in the same model, although there was

an association between these two variables. This is not problematic, however, because the effect of brood WL₁₄ did not change drastically when brood BM₁₄ was removed from the model and brood BM₁₄ was positively associated with brood age at fledging, while brood WL₁₄ was negatively associated.

Fledging Asynchrony

There were large differences in fledging asynchrony between broods. Against our expectations, we did not find fledging asynchrony was related to within-brood variation in wing development, implying that fledging was not triggered by the wing development of the fledglings. Yet, when analysed in more detail we did find that the time between the moments of fledging of two successive fledglings showed a positive trend with the difference in their wing development. This trend might imply that the larger the difference in development between fledglings, the more time there was between their fledging moments.

Sex-specific Fledging Strategies

For both the age of fledging and fledging order, wing length seemed to be important. If there were a fitness benefit for fledging earlier and/or fledging as the first of a nest, we would expect nestlings to invest in wing development rather than, for instance, body mass. Nilsson & Svensson (1996) experimentally showed that, under competition, the wings of smaller nestlings grow at a rate expected for their age, but at the cost of a reduced increase in body mass. In this way, the smaller nestlings keep up better with the wing length of larger nestlings, suggesting that wing development has priority over body mass gain. We found that the sexes differed in BM₁₄ but not in WL₁₄. Along similar lines, we hypothesize that it may be adaptive for females to allocate relatively more resources to wing development to ensure either earlier fledging or fledging as one of the first in the nest.

Fledging Order

Fledging order depended on relative WL₁₄. This result agrees with most studies in passerines (Nilsson 1990; Michaud & Leonard 2000; Johnson et al. 2004). We also found that the first fledged young spent more time in the nestbox opening immediately before fledging than its nestmates. These results contradict Lemel's (1989) idea that competition between nestmates caused fledging and subordinate young fledge first to break the monopolization of the nestbox opening by the dominant siblings. Perhaps local environmental factors led to much more severe competition between nestmates in Lemel's (1989) study than in the other studies, resulting in a stronger effect of body mass on fledging order.

Both relative BM₁₄ and swapping contributed almost significantly to the model when these parameters were added to the model separately (Table 3). The close to significant negative association between relative BM₁₄ and fledging order indicates that body mass might play a role in fledging order, but the effect size of relative BM₁₄ is much smaller than of relative WL₁₄. The almost significant positive association between swapping and the fledging order is particularly interesting. If not by chance, this effect of swapping must be caused by a difference between the swapped and nonswapped nestlings. The difference may be either a response to the swapping procedure or a consequence of nonrandom selection by the experimenter. We cannot distinguish between these explanations. For all measured traits, with the exception of fledging order, swapped and nonswapped individuals did not differ. Of course, responses or nonrandom selection can be related to nestling traits that we did not measure. Because both relative BM₁₄

and swapping did not improve the model, were not significant and had an effect size that was at least two times smaller than the effect size of wing length, we did not incorporate them in the final model.

Conclusions

Sex and BSR did not influence timing and age of fledging of the brood. Age of fledging depended highly on wing development, which suggests that nestlings wait to reach a certain state of development before fledging. To fledge in synchrony, nestlings should keep up with their nestmates during development. Therefore, we hypothesize that it may be adaptive for females to allocate relatively more resources to wing development to ensure fledging at the same time as their male siblings. Our finding that BSR and nestling sex did not affect the timing and order of fledging is consistent with this view. To investigate the adaptiveness of timing and order of fledging, studies are needed to look at the consequences of these for survival.

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